ALLELOPATHY

Definition and Concept

According to Ferguson and Rathinasabapathi, "allelopathy refers to the beneficial or harmful effects of one plant on another plant, both crop and weed species, by the release of chemicals from plant parts by leaching, root exudation, volatilization, residue decomposition and other processes in both natural and agricultural systems."

First, some definitions that relate to allelopathy.

- **Allelochemical**–for the purposes of this article, a toxic chemical produced by a plant
- **Phytochemical**–a chemical compound that occurs naturally in a plant
- **Toxicity**–the negative effect of a substance on a plant
- **Synthetic herbicide**–herbicides formed through a chemical process or chemical synthesis

With the continuing, increasing occurrence of herbicide-resistant (HR) weeds in agricultural systems, there is renewed interest in determining how/if allelopathy might be used as a possible option in weed control systems.

Allelopathic effects can be and have been measured in controlled environment settings such as a laboratory or greenhouse, but replicating the effects in the field has been and continues to be difficult.

Research has left little doubt that the presence of a phytochemical that is toxic to plants of another species will have an adverse effect on those plants. However, equating the toxicity of the phytochemical to its availability and effect in the natural environment of the target plant species is often not accomplished.

According to Colquhoun, effective demonstration of allelopathy on plant growth and development and its reliable application in agricultural pest management have been minimal. The use of allelopathic cover crops such as rye has resulted in the greatest application of allelopathy in agriculture.

Very little is known about the mode of action of allelochemicals or how plants of a particular species avoid reputed allelochemical effects in a natural setting. Even though there is a growing body of literature that implicates allelopathy in plant-to-plant relationships and interactions in a natural agricultural setting, the translation of this knowledge into its use or place in managing weeds in agricultural production systems has been slow.

The study of allelopathy and discerning its importance for agricultural production systems will only be advanced if current and forthcoming research results can be translated into new technologies that can be used for weed management and/or reduced dependence on synthetic herbicides.

History and Future

Dr. Stephen Duke, USDA-ARS Research Leader at Oxford, MS, published an excellent summary on the current status of research on allelopathy and the possible implications for agriculture. His commentary article was published in 2010 in Vol. 25 of the "Allelopathy Journal". Below are summary points taken from this article.

- Results of past research with allelopathy most often have demonstrated correlative rather than cause and effect relationships.

- Effects often attributed to allelopathy may actually be a result of competition for resources between/among plants.
- There is evidence that chemical detection of a competing plant species can trigger the production of an allelochemical.
- Past research has often shown that many plants produce compounds that, in high enough concentrations, are toxic to other plants in the absence of soil. Such experiments suggest the potential for but do not prove allelopathy in a natural setting.
- Extrapolation of results from experiments conducted in a laboratory setting in the absence of soil is virtually impossible.
- Allelochemicals from living plants and dead plant matter are constantly entering the soil environment and this is almost impossible to measure. Also, these allelochemicals are either absorbed in the water portion of the soil or are adsorbed to soil particles, so the amount of the allelochemical that is available at any one time is difficult to measure or predict.
- Reputed allelochemicals are often inactivated in a soil environment due to their instability, degradation by soil microbes, or other interactions with soil. Also, those that are water-soluble are subject to leaching from the root zone of potential target species.
- Methods that are being developed can be used to determine if the loss of allelochemicals from the soil due to the above processes is offset by the producing plant's exuding or secreting more of the allelochemical.
- Allelochemicals that are steadily produced by a donor plant and released into the soil may not seem too significant, but may become so if this steady release and subsequent accumulation of the allelochemical by the receiving plant is in an amount to cause an adverse reaction. In other words, a steadily produced source of an allelochemical that is toxic to a receiving plant is more important than the static concentration of the toxic allelochemical in the soil at any measurement period.
- Determining/understanding the mechanisms of allelopathic activity, followed by utilizing that information to manage weeds in agricultural systems, is the challenge that is faced by scientists.
- Transgenically imparting or enhancing allelopathy in crop species will be a positive step toward utilizing allelopathy in agriculture.
- Research is needed to ascertain soil microbial involvement in allelopathy; e.g. do soil microbes transform allelochemicals to more or less toxic forms, does exposure of soil microbes to a particular allelochemical over a period of time increase their activity on the allelochemical, do allelochemicals change the soil microbial makeup.
- Increased interest in allelopathy is fueled by the need to reduce synthetic herbicide use in agriculture, and the desire to find or identify natural products or allelopathic processes to control HR weeds.
- Using transgenics to produce crop cultivars that have enhanced allelopathic properties is being undertaken, but this area of research is insignificant compared to that of using transgenics to develop herbicide resistance in crop species.
- In the near future, there is little reason to expect the development of allelochemicals for use as natural herbicides.

Wheat Allelopathy

Soybean–wheat doublecropping is an important cropping system in the Midsouth.

An often-stated allelopathic effect is that of wheat straw on soybeans that follow wheat in a doublecrop system, or that of wheat straw on weed seed germination and emergence.

A summary of the results from an extensive literature search follow.

- Both wheat residue and wheat seedling allelopathy are currently being researched for their potential utilization in weed management.
- Results reported from greenhouse experiments where wheat straw or wheat straw leachate was used have shown a perceived adverse allelopathic effect of wheat straw on early growth of soybeans.
- Results from field studies using the same variables as those used in greenhouse studies are not correlated with those of the greenhouse studies; i.e., the same results have not been obtained from field studies.
- In field studies where leaving wheat straw on the soil surface or incorporating the straw into the soil resulted in stunted early growth of soybeans, adding supplemental N at soybean planting overrode the effect. In treatments where wheat straw was removed or burned, the effect did not occur. Thus, N immobilization rather than allelopathy was likely responsible for the measured effects.
- Wheat plants produce and release toxic substances that inhibit several weed species, and many of these compounds have been identified. This has led to the perception that wheat allelopathy has the potential for the management of weeds.
- It is believed that the constant exposure of weed plants to continuously released toxic allelochemicals would create a stress environment for the weeds, thereby resulting in a reduced impact of the target weed in a cropping system.
- Wheat accessions/genotypes/varieties differ in their allelopathic effect toward other plant species.
- Research on wheat allelopathy towards weeds has progressed to the identification of wheat allelochemicals, and further to the identification of genetic markers associated with this trait. Presently, there is no significant agronomic achievement resulting from this knowledge.
- Wheat varieties have not been developed that have enhanced biosynthesis of allelochemicals for weed control, although this field of research and development is of interest to a number of researchers.

In summary, there is no evidence that the phytotoxicity of wheat straw on soybeans is a field problem. Thus, perceived allelopathy effects that were measured in the greenhouse but not in field environments are likely tempered by the soil environment. Also, N immobilization by the wheat straw probably results in lack of sufficient available N needed for early-season soybean growth before nodulation and subsequent N fixation occurs.

Even though past research indicates that wheat varieties release allelochemicals that have an adverse effect on some weed species, this has not led to a weed management system that incorporates this concept.

A 1982 "Weed Science" article states that further screening of different weed species against wheat allelopathic toxins in field situations is needed before wheat allelopathy can be a factor in weed control. This is still true.

A statement from Molecular approaches in improving wheat allelopathy published in 2005 is "Wheat allelopathy has great potential in integrated weed management systems. Concerted research efforts have been made toward the development of wheat varieties with high allelopathic activity". However, wheat varieties that may have been released with this trait are not advertised in the US.

Articles used to develop the above summary about wheat allelopathy are:

Techniques for identifying tolerance of soybean to phytotoxic substances in wheat straw, by Herrin, Collins, and Caviness ("Crop Science", Vol. 26, 1986).

Soybean-Wheat Doublecropping: Implications from straw management and supplemental nitrogen by Hairston, Sanford, Pope, and Horneck ("Agronomy Journal", Vol. 79, 1987).

Molecular approaches in improving wheat allelopathy, by Wu.

Allelopathy in wheat, by Wu, Pratley, Lemerle, and Haig ("Ann. Appl. Biol.", Vol. 139, 2001).

Allelochemicals in wheat: cultivar difference in the exudation of phenolic acids, by Wu, Haig, Pratley, Lemerle, and An ("J. Agric. Food Chem.", Vol. 49, 2001).

Evaluation of seedling allelopathy in 453 wheat accessions against annual ryegrass by the equal-compartment-agar method, by Wu, Pratley, Lemerle, and Haig ("Aust. J. Agric. Res.", Vol. 51, 2000)

Allelopathic potential of wheat straw on selected weed species, by Steinsiek, Oliver, and Collins ("Weed Science", Vol. 30, 1982).

Corn Allelopathy

Corn allelopathy arguably has received less attention than allelopathy of other crops such as rice, wheat, and grain sorghum.

Since corn is often rotated with soybeans in the Midwest, and is increasingly so in the Midsouth, the effect of possible corn allelopathy on following soybeans is of interest to Midsouth producers. However, there is negligible information to indicate any such effect.

So, the points below are statements about possible corn allelopathy in general.

- As with extracts from the residues of other crops, extract from corn residue inhibits germination, growth, and development of corn seedlings in laboratory experiments (Martin, McCoy, and Dick, "Agron. Journal", Vol. 82, 1990; Elmore and Abendroth). However, there is no indication in the literature that this has been manifested in a field environment.
- Using corn allelopathy is a hoped-for and perceived possible alternative to weed management with synthetic herbicides or herbicide-resistant hybrids (Pratley 2006). This is a worthwhile alternative weed management approach in corn, but it has not been successfully accomplished in production environments.
- In field experiments, Elmore and Abendroth state "...yields are reduced when corn follows corn....", or to use common jargon, there is a "yield drag" for corn following corn. Allelopathy is often implicated but rarely if ever proven in field environments because of weather vagaries, amount and makeup of the residues, and unknown factors such as soil microbial activity. More than likely, allelopathy is used as a catch-all term for the myriad unidentified causes of this proven

occurrence.

According to Heggenstaller (Pioneer, 2012), "corn residues are a major factor contributing to lower yields for corn following corn compared to corn rotated with soybean, particularly in no-till management." Major points from this study are:

- With corn following corn, residue management seems to be the key to avoiding the yield-reducing effects of corn stover. This involves offsetting stover's potential for producing negative effects by reducing the interference from corn residue through removal (baling) of a portion (approximately one-half) of the stover.
- Results suggest that corn after corn with stover removal may produce yields that are similar to those from corn rotated with soybeans.
- No-till continuous corn production is amenable to stover removal due to the high amounts of residue that are produced and remain on the soil surface in the absence of tillage.
- It is proffered from previous research that as much as half of the corn residue can be removed without negatively affecting the beneficial effects of that residue.

Additional discussion of possible corn allelopathy is presented by Lykins in the April 2012 issue of "Corn and Soybean Digest".

In summary, and to be concise, corn allelopathy has not been specifically identified as a factor in US corn production systems, especially as it relates to soybeans rotated with corn. There is no evidence that corn allelopathy will be utilized as a weed management tool in the near future.

Sorghum Allelopathy

Grain sorghum is not a major crop acreage-wise in Mississippi, with only 115,000 acres harvested in 2015 and only 11,000 acres harvested in 2016. However, it is recognized as being superior to corn in both drought and heat tolerance (Crop Management, Nov. 2010). Therefore, it has the potential to become a significant rotation partner with soybeans in a dryland production system.

The recent incursion of the sugar cane aphid into Midsouth sorghum fields may further limit sorghum production in the region, either because of its negative effect on sorghum yield or the increased cost of production associated with its control.

Above, it was stated that corn allelopathy arguably has received less attention than has allelopathy of other crops. Conversely, sorghum allelopathy has received considerable attention. Sorghum's allelopathic properties are more pronounced than those of most other plants that have been studied.

Research findings are presented here to support sorghum's allelopathic effect and the potential usefulness of that property in cropping systems.

A set of publications from the USDA-ARS Natural Products Utilization Research Unit in Oxford, MS provides results from a continuing investigation of sorghum's allelopathy. Scientists responsible for these publications are F. Dayan, I. Alsaadawi, A. Rimando, Z. Pan, S. Baerson, A. Bimsing, S. Duke, L. Pratt, D. Cook, and I. Kagan.

- Sorgoleone with its lipid resorcinol analogue is a potent phytotoxin produced by grain

sorghum root hairs, and likely accounts for much of the allelopathy attributed to sorghum. Sorgoleone is one of the most studied allelochemicals.
- Increased production of sorgoleone by sorghum roots was measured when a crude extract from velvetleaf roots was added to the growth medium.
- Sorgoleone can be absorbed through the hypocotyl and cotyledonary tissues of germinating seedlings, thus leading to the possibility that its effects are the result of photosynthesis inhibition in young seedlings.
- Research results suggest that sorghum roots have the capacity to continuously exude sorgoleone into the soil. As this phytotoxic exudate is released directly into the soil, its action is similar to that of a soil-applied herbicide.
- The potential for continuous exudation of sorgoleone into the soil may sustain its presence and subsequent activity in soil over a much longer period than that of an applied herbicide.
- Sorgoleone is persistent in soil, but it is mineralized by microorganisms over time.
- Scientists at the above USDA-ARS Unit are developing information needed to genetically increase production of sorgoleone in sorghum.

Einhellig and Rasmussen reported in the "Journal of Chemical Ecology" (Vol. 15, 1989) that a grain sorghum crop reduces weediness in the following crop year compared to corn and soybeans. This effect was primarily on broadleaf weeds, and involved both delayed emergence and growth inhibition of weeds during the growing season. They concluded that allelopathic conditions from growing grain sorghum must be considered as a major factor in weed inhibition, and that this has potential applications in production agriculture.

Wortman, Schmidt, and Lindquist (Crop Management Vol. 13, Dec. 2014) conducted experiments with sudangrass (*Sorghum bicolor* (L.) Moench var. sudanense) in a range of soil mixtures. A summary of their results follows.

- Sudangrass root exudates and shoot residue both reduced emergence of green foxtail grass from soil.
- Sudangrass root exudates and decomposing shoot residue acted synergistically to delay emergence of green foxtail from soil.
- These results indicate that sudangrass has the potential to provide measurable reductions in grass weed seed emergence from soil. The resulting recommendation is that producers use sudangrass as a cover crop and incorporate both shoot and root residues into the soil to realize maximum weed suppression effect.

Roth, Shroyer, and Paulsen (Agronomy Journal, Vol. 92, 2000) reported that wheat yields following grain sorghum were reduced by 15 and 30% compared to fallow when the sorghum residue had been tilled or left on the soil surface with no tillage, respectively. Their results suggest that tillage of the sorghum stover abated but did not completely offset the effect of the allelopathic compounds in the sorghum stover. They found no differences in tolerance to sorghum residue among wheat hybrids.

In summary, there is strong research evidence that sorghum has an allelopathic effect on plants of a following crop, and on weed plants that may appear in a growing sorghum crop.

It is anticipated that sorghum's allelopathic effect will be the first to be exploited for use in production agriculture. However, the application of this trait has yet to be realized. Certainly, this property of sorghum needs further attention so that its potential for use in weed control and curtailing the use of synthetic herbicides can be determined and hopefully become a reality.

Cover Crops and Allelopathy

Cover crops have long been recognized for their potential to provide soil cover that will curtail erosion between crop growing seasons, and to provide residue that is available to increase soil organic matter.

With the increasing occurrence of HR weeds, cover crops are now being evaluated for their allelopathic potential to control weeds.

Current thought is that cover crops and their residues may provide weed suppression through their physical presence on the soil surface and/or by the release of allelochemicals that may inhibit weed seed germination and/or early seedling development (Weston, "Agronomy Journal", Vol. 88, 1996; Weston, 2005). Weston also suggests that allelopathic crops offer potential for the development of herbicides, as well as for providing germplasm from which to select for allelopathic products and chemistry.

Thus, allelopathic potential of cover crops for weed suppression is touted, and research has shown that cover crop extracts can inhibit early plant development (Kelton, Price, and Mosjidis, Intech Press, 2012; Wortman, Schmidt, and Lindquist, Crop Mgmt., 2014).

In a study by Petersen et al ("Agronomy Journal", Vol. 93, 2001), isothiocyanates released by a turnip-rape mulch were determined to suppress weed germination after incorporation of the mulch into the soil. They concluded that the potential of cover crops to release these compounds should be further investigated as a tool for weed control/suppression in integrated cropping systems.

In a report in "Agronomy Journal" (Vol. 104, 2012), Lawley, Teasdale, and Weil determined that early and competitive fall growth of a forage radish cover crop is the dominant mechanism for early-spring weed suppression resulting from use of this species as a cover crop. They did not measure any allelopathic activity that limited seed germination or seedling development. Thus, they concluded that cover crop management strategies should be directed towards practices that ensure maximum cover crop development in the fall to ensure maximum physical weed-suppression activity the following spring.

Cereal cover crops will produce more biomass than will legume cover crops (Reddy, "Weed Technology", Vol. 15, 2001). This increased physical barrier, coupled with the slower degradation of residues from cereals compared to that of legumes, should result in more and longer-lasting weed control/suppression from using cereal cover crops.

There are five important points regarding the use of cover crops for weed control either by physical suppression or by allelopathy.

- Differentiating between allelopathy and the mulching effect of cover crops is difficult. As stated above, it is accepted that increased cover crop biomass on the soil surface can suppress weeds, but to what extent and with what resulting value in a soybean production system is not known.

- The variability in allelopathic effects from plant residues presently negates their consideration as a stand-alone weed control option in large-scale crop production systems.
- A likely system will be using cover crops that are proven to physically or allelopathically suppress weeds to offset some herbicide use.
- The additional cost associated with using cover crops in a crop production system must be considered (Reddy, "Weed Technology", Vol. 15, 2001). In other words, the additional cost of using cover crops for potential weed control must be compensated for by increased soybean yield and/or reduced herbicide usage/cost. Otherwise, producers will be reluctant to insert cover crops into soybean production systems for any reason.
- To maximize the weed-suppression capacity of an allelopathic cover crop such as sudangrass, shoot residues should not be removed by grazing or haying (Wortman, Schmidt, and Lindquist, Crop Mgmt., 2014).

Summary

Increased interest in allelopathy is fueled by the desire to reduce synthetic herbicide use in agriculture and to find or identify natural products or allelopathic processes to control HR weeds.

Allelopathic effects can be and have been measured in controlled environment settings such as a laboratory or greenhouse, but replicating the effects in the field has been and continues to be difficult.

Research has left little doubt that the presence of a phytochemical that is toxic to plants of another species will have an adverse effect on those plants. However, equating the toxicity of the phytochemical to its availability and effect in the natural environment of the target plant species is often not accomplished.

Research is needed to ascertain soil microbial involvement in allelopathy; e.g. do soil microbes transform allelochemicals to more or less toxic forms, does exposure of soil microbes to a particular allelochemical over a period of time increase their activity on the allelochemical, do allelochemicals change the soil microbial makeup.

Concerted research efforts have been made toward the development of wheat varieties with high allelopathic activity. However, wheat varieties that may have been released with this trait are not advertised in the US.

Corn allelopathy has not been specifically identified as a factor in US corn production systems, especially as it relates to soybeans rotated with corn. There is no evidence that corn allelopathy will be utilized as a weed management tool in the near future.

There is strong research evidence that sorghum has an allelopathic effect on plants of a following crop, and on weed plants that may appear in a growing sorghum crop. It is anticipated that sorghum's allelopathic effect will be the first to be exploited for use in production agriculture. However, the application of this trait has yet to be realized.

The variability in allelopathic effects from plant residues presently negates their consideration as a stand-alone weed control option in large-scale crop production systems.

Cover crops that are proven to physically or allelopathically suppress weeds to offset some herbicide use may be a consideration in a soybean production system. However, the costs associated with this practice and the uncertain magnitude of the effect from using this practice will affect its adoption.

The likelihood of weeds becoming resistant to allelochemicals is unknown, so if they become an important component in weed management, this will be a factor to consider.

Allelochemicals that may be forthcoming will have to be selective in their effect; i.e., they must only adversely affect targeted plants such as weeds.

Using transgenics to produce crop cultivars that have enhanced allelopathic properties is being undertaken, but this area of research is insignificant compared to that of using transgenics to develop herbicide resistance in crop species.

In the near future, there is little reason to expect the development of allelochemicals for use as natural herbicides.

The principle of allelopathy may have the greatest application in low-input agricultural systems.

The study of allelopathy and discerning its importance for agricultural production systems will only be advanced if current and forthcoming research results can be translated into new technologies that can be used for weed management and/or reduced dependence on synthetic herbicides.

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